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ON THE STRUCTURE OF THE TEETH OF THE DEVONIAN CLADODONT SHARKS.

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The Fishes that bear the above name have until quite recently been known to us only by their teeth which abound in some of the limestones of the Lower Carboniferous System. They are equally abundant on the same horizon in Europe. A few have been described from the underlying Devonian strata. But everywhere below the Carboniferous rocks they have proved extremely rare. Indeed with the exception of perhaps a half dozen detached teeth none were known until recently. Moreover even this scanty knowledge of the teeth was surpassed by our still scantier knowledge of the fishes that wore them. With the appearance of Dr. Newberry's Monograph of Fossil Fishes in 1889, we made our first acquaintance with the Cladodonts in the flesh. A badly mutilated and very imperfect fossil was there figured under the name of *Cladodus Kepleri* from which our conceptions of these almost primæval sharks first took a distinct form. Another to which the name *Cl. Fyleri* was attached served only in general to confirm the other, being too confused and crushed for description.

At about the same time Dr. Traquair, of Edinburgh, described to the Geological Society of Glasgow another even more faulty specimen which had come to light from the Carboniferous Limestone of Scotland, thus affording another illustration of the now familiar truth of the double discovery of an important fact by two independent workers at or very nearly at the same time.

Up to the date above mentioned all that we could do was to infer from the nature of the teeth the character and form of their wearers and these inferences have been in great part supported and in some degree corrected by the discovery of the fish. That they were shark-like was a necessary conclusion, but the details of their structure we owe entirely to these recent discoveries above alluded to—the work for the most part of Dr. W. Clark, of Berea, Ohio. I need scarcely add that even this newly acquired knowledge is very incomplete and much yet remains to be learned. The fossils are embedded in a most refractory matrix of hard concretionary shale impregnated with iron pyrites. They are themselves highly pyritized so that the labor of extricating them bit by bit and then of recementing the hundreds of fragments into which they are usually broken in the process, is one demanding the utmost care and patience, with a liberal allowance of time and eyesight.

Descriptions of the fossils thus obtained have appeared in various numbers of the American Geologist during the past two years (1893 and 1894), to which the reader is referred for further details of the structure of the animal. The present paper proposes to deal only with their teeth—the *Cladodus* of the palaeontologist—for it must be borne in mind that in thus naming a fossil tooth no assumption is made concerning the fish nor is it pretended that the two genera—the tooth and the fish—should coincide. Teeth from different parts of the same animal may and often do vary in shape and while each form has been described and named it may and probably will be found that two or even more of these species of teeth, the *Cladodi*, were set in the mouth of a single fish. In this case, as has frequently happened before, the superfluous names will be dropped or used in some subordinate sense and the name most closely defined and most readily recognized will be retained for the animal itself.

These preliminary remarks will suffice to show the relations of the subject of the present paper. I may further add that teeth are not sufficiently abundant or in sufficiently good condition to allow their free use for sectioning. As already stated the fossils are heavily pyritized and though this applies less to the teeth than to the bones yet if it were not for a fortunate accident I should have been unable to present the details herewith given.

During the prosecution of his researches, Dr. Clark was fortunate enough to discover a small nodule of claystone loaded with a number of cladodont teeth. The matrix being soft and the teeth hard and free from pyrites I was enabled to extract them and orient them for grinding. Moreover the material being free from the dense opacity of pyrites the structure was more easily made out.

I. THE GENERAL FORM.

The general form of a cladodont tooth is a long, sharp and usually somewhat bent median cusp with one or more denticles on each side of it. These are all set on a flat semicircular or crescentic base on which they stand almost at right angles. They are not central on this base but lateral, that is they stand on the outer edge and indeed often slightly overhang it. The middle of this edge is a little excavated and in the recess thus formed lies the tip of the cusp of the succeeding tooth ; for as in modern sharks the teeth grew in ranks and advanced over the edge of the jaw from the inside outward. All these facts are abundantly proved by specimens in the collection of the discoverer.

The figures I and II show the typical form of a Cladodus and its chief varieties, and as will be seen the denticles range in number from almost zero to several on each side of the median cusp. As with modern sharks they were set by the base on a membrane with which they maintained a living connection and had no union with the bone or bony cartilage of the jaw.

II. TISSUES OF THE TEETH.

Beginning with the flat expanded semicular or crescentic base of the Cladodus, a longitudinal section shows us that the fundamental tissue of the tooth is loose and spongy, especially so on its lowest layer where connection is maintained with the subjacent membrane. In some sections where the tissue is cut transversely it assumes the appearance of a mass of thick-walled cells filled with a lighter substance or rather of semi-perforations in a somewhat dense membrane, very irregular in size and in shape. This fundamental tissue increases in density upwards. The cavities become smaller and are arranged rather more regularly so as to give the appearance of lying in rows. In the cusp, which is composed of tissue of the same nature, a still further condensation takes place accompanied we may safely infer with a higher degree of hardness. The clear demonstration of this tissue is frequently difficult in consequence of the changes induced by fossilization. It may often be seen in only a small part of a tooth. But it may be traced from the basal layer almost to the very tip of the cusp.

Scattered through this fundamental tissue may be seen the Haversian canals of large size and running in all directions through the mass of the bone. They present no unusual appearance but are perhaps more numerous near the base than elsewhere. Around each can be seen the concentric lamination generally accompanying them. The inner portion of these laminae to a distance about equal to the width of the canal on each side is apparently denser than the rest and shows a distinctly darker tint.

No lacunae are present in these lamellae, or indeed anywhere in the tooth. Nor are the canalicules abundant though a few may now and then be seen radiating from the Haversian canals into the substance of the tooth through the denser layer already mentioned that surrounds the canals.

As lacunae are not present there are no subordinate canalicules with which those that issue from the canals can inosculate and their extent is consequently limited to the region immediately around the canals from which they issued. It may be that the spongy nature of the fundamental tissue superseded the necessity for the permeation of the whole tooth by these minute channels of communication and of nutrition.

Fig. III shows a longisection of a Cladodus. The dark spots represent sections of the Haversian canals scattered through the lighter fundamental tissue. The red layer represents the superficial dentine. Colors of course conventional.

Fig. IV shows on the left the tip of a Cladodont tooth with the fundamental tissue traversed by Haversian canals and the superficial dentine crossed by innumerable tubules diverging from these canals. On the right is shown a still more magnified view of the same structure.

Beside the fundamental tissue and outside of it is another, or perhaps I should rather say that there are two others enclosing it and fitting it to do the work of a tooth. This outer layer is denser than the other and differs from it in several respects. It contains no Haversian canals though these are abundant and large to its very base. Indeed this layer frequently rests upon an anastomosing series of them. From this or from any of the canals lying near the outer surface of the fundamental tissue rise large numbers of minute tubules (canalicules), which at first diverge and afterwards become parallel and run out toward the surface branching and becoming more numerous and delicate as they approach it. This gives to the outermost layer a peculiar appearance under the microscope closely resembling that of dentine especially of the form called osteodentine or ivory. It is difficult to affirm that the tubules actually reach and open upon the surface but this is probably the case.

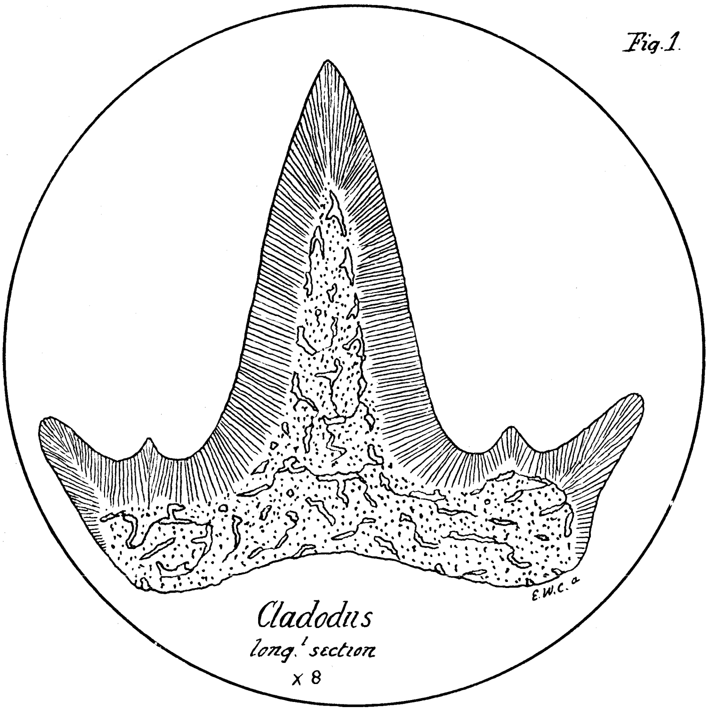
This layer, though its structure is identical throughout, may yet be divided as above suggested into two strata if not more. It frequently shows a tendency to divide in this way spontaneously. The lamination appears to be determined by the planes of forking of the tubules which takes place at certain definite levels in the dentine. This, at least, may reasonably be inferred from the coincidence of the planes of bifurcation of the tubules, and that of the lamination of the layer.

III. ABSENCE OF ENAMEL.

No trace of any substance that can be called enamel is visible on any part of these teeth. This which is the hardest and most earthy of all the animal tissues is easily recognized by its peculiar crystalline appearance and fracture. In the teeth of the Cladodonts the dentine above described is the outermost layer. If this was the case with all the Devonian Cladodonts we may conclude that the highest form of tooth-tissue had not at that date been reached by this family. This is the more noteworthy as the teeth of the Eocene sharks, Carcharodon, for example are faced with a thick layer of prismatic enamel, as are also those of the existing species.

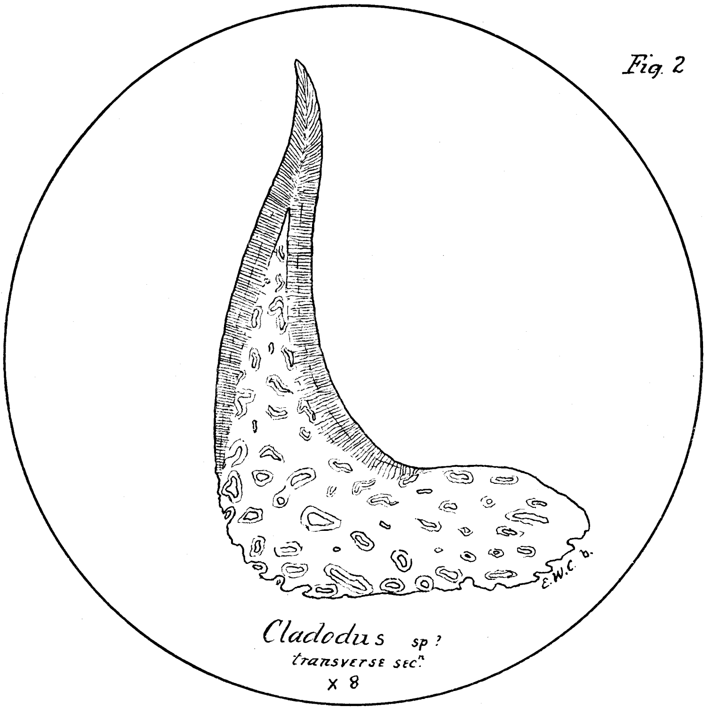
PLATE I.

Fig. 1



Cladodus
long.^{l} section
x 8

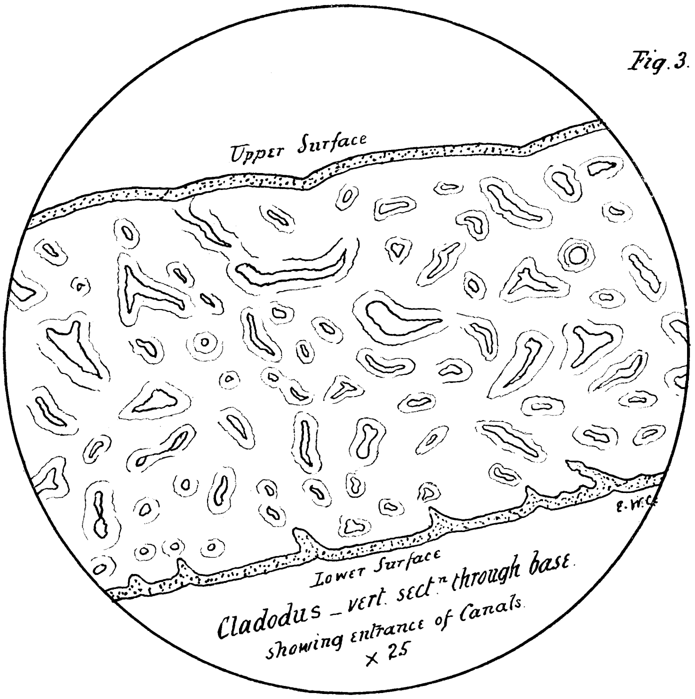
Fig. 2



Cladodus sp?
transverse sec.^{n}
x 8

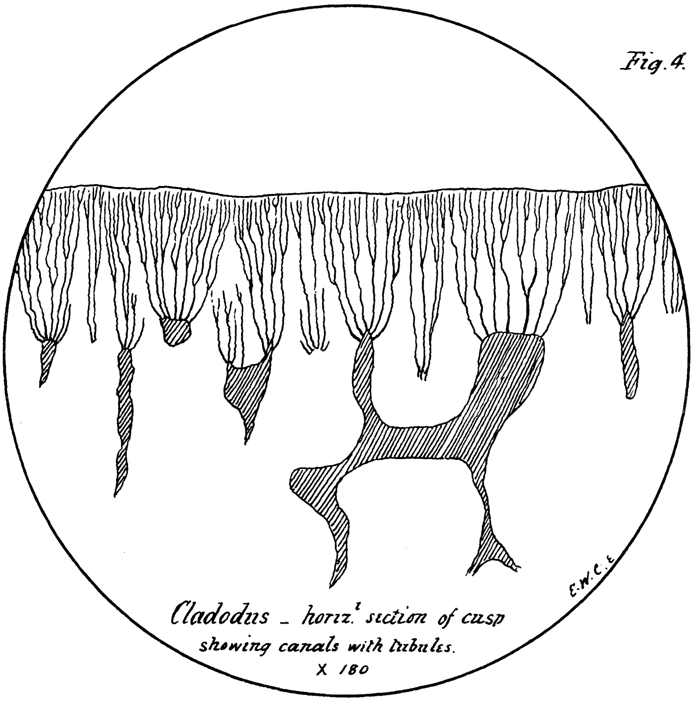
PLATE II.

Fig. 3.



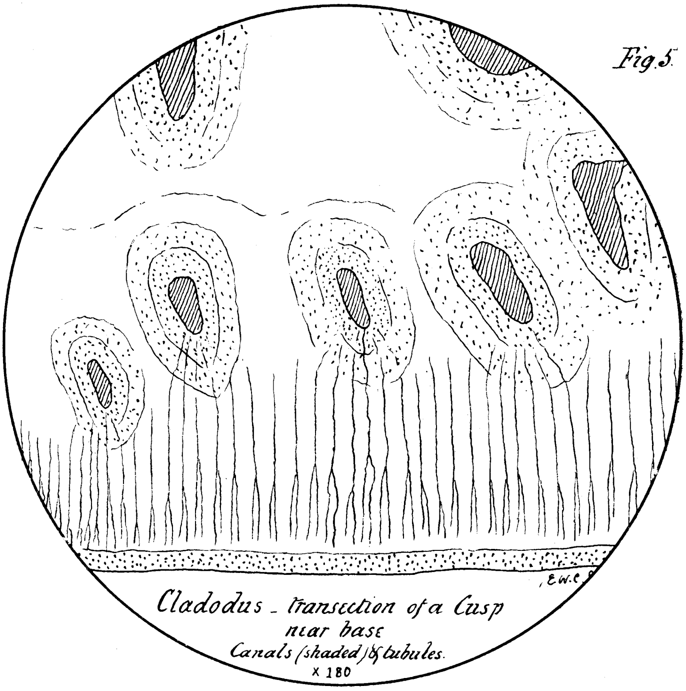
Cladodus – vert. sectn through base.
showing entrance of Canals.
× 25

Fig. 4.



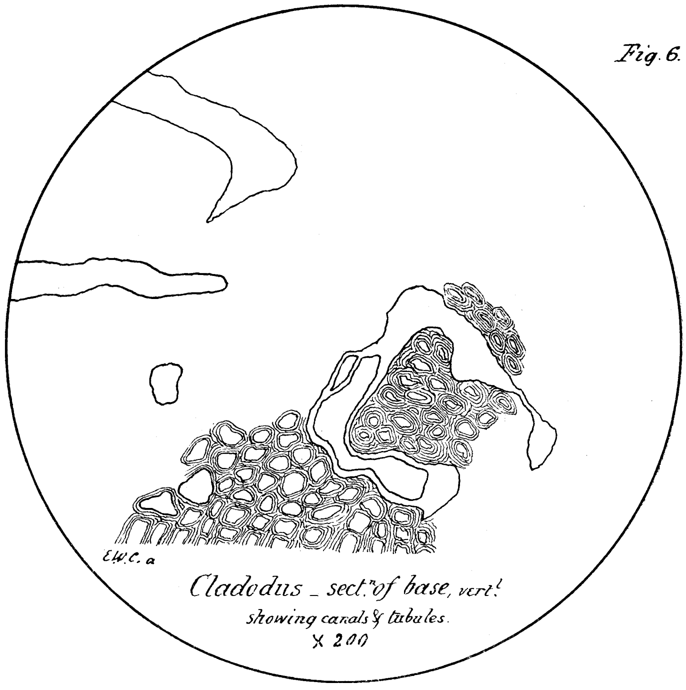
Cladodus – horizl. section of cusp
showing canals with tubules.
X 180

Fig. 5.



Cladodus _ transection of a Cusp
near base
Canals (shaded) & tubules.
X 180

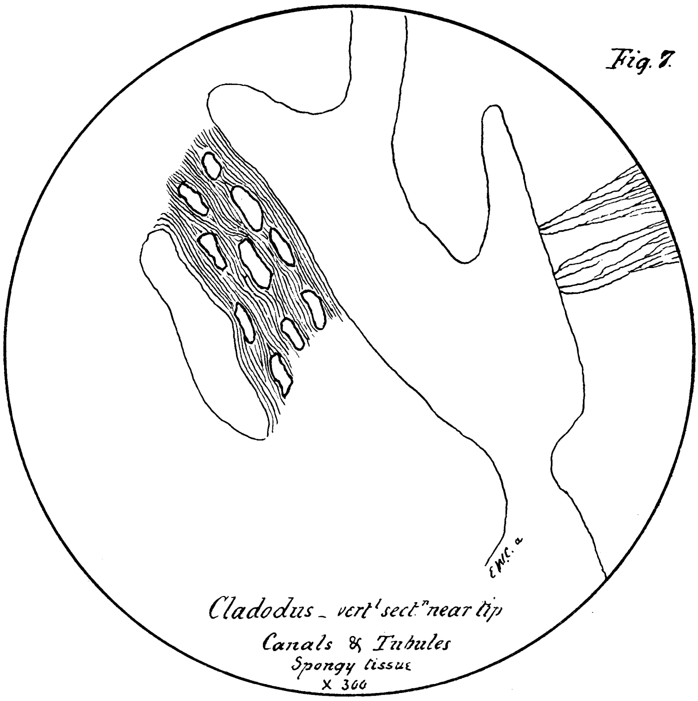
Fig. 6.



Cladodus _ sect.^{n} of base, vert.^{l}
showing canals & tubules.
X 200

PLATE IV.

Fig. 7.



Cladodus _ vert^{l} sect.^{n} near tip
Canals & Tubules
Spongy tissue
X 300